# Forest Invasion by the African tulip tree (Spathodea campanulata) in the Hawaiian Islands: Are Seedlings Shade-Tolerant?

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**Forest Invasion by the African tulip tree (*Spathodea campanulata)* in the Hawaiian Islands: Are Seedlings Shade-Tolerant?**

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**Abstract:** Native to West Africa, *Spathodea campanulata* (African tulip tree) is frequently viewed as a shade-intolerant invader. It commonly colonizes roadsides, human-disturbed forests and abandoned agricultural land in tropical islands, where it can then become dominant in secondary forests. Some authors have suggested that the seedlings may be shade-tolerant and able to establish in closed forest, but the shade tolerance of seedlings has never been evaluated. We identified tolerated light environments of *S. campanulata* seedlings in wet forests in Hawaii by measuring photosynthetically active radiation (PAR) around naturally occurring seedlings (< 30 cm height) in the field. We also measured photosynthetic responses of seedlings to light under field and lab conditions, and determined seedling growth rates in sun and shade. Seedlings were found in shaded conditions in the field, and they consistently had positive net carbon gain at 50 μmol photons $m^{-2}\cdot s^{-1}$ PAR, with an estimated mean compensation point below 10 μmol photons $m^{-2}\cdot s^{-1}$, indicating high shade tolerance. The most frequent midday light environments of *S. campanulata* seedlings in the field were in the range around 50 to 200 μmol photons $m^{-2}\cdot s^{-1}$ PAR, i.e., 2.5% to 10% of full sunlight. Among seedlings found growing in shade, minimum saturating light ($E_k$), determined from chlorophyll fluorescence, averaged 260 μmol photons $m^{-2}\cdot s^{-1}$, suggesting that seedling maximum photosynthesis can occur at less than 13% of full sun. Growth rates of young seedlings in shade and sun were comparable. Widespread wind dispersal of seeds, seedling tolerance of low light, and our observations of some *S. campanulata* saplings establishing in rainforest without recent disturbance suggest that *S. campanulata* will be a persistent component of Hawaiian lowland rainforests.

## Introduction

Many studies show that invasive species can pose important threats to native biodiversity (Hierro et al. 2005, Mack et al. 2000) or cause major problems in natural ecosystems (Merlin and Juvik 1992), especially on tropical islands (Daehler 2005, Denslow 2003, Loh and Daehler 2007, Kueffer et al. 2010, Meyer and Florence 1996, Meyer 2004, Reaser et al. 2007). The invasiveness of introduced plants in new geographic areas has been explained by characters such as competitive advantages under particular environmental conditions (Daehler 2003, Mooney et al. 2005), or possession of novel chemical traits compared with the native flora in the introduction area (Callaway and Ridenour 2004). Certain invasive plants, such as *Spathodea campanulata*, have attracted particular interest because of their successful spread across numerous tropical islands (Labrada and DiazMedina 2009).

*Spathodea campanulata* P. Beauv. (Bignoniaceae), commonly called African tulip tree, is widely naturalized in many Pacific islands and considered a threat to native biodiversity (Meyer 2000, Pacific Islands Ecosystems at Risk 2011), notably by creating a shading effect, which reduces native species richness under its canopy (Weber 2003). It is also reported as a serious agricultural weed, especially in coffee plantations (Labrada and DiazMedina 2009). Forests dominated by *S. campanulata* are frequently established in the lowland tropics on abandoned agricultural lands, deforested lands (Francis 2000, Labrada and DiazMedina 2009, Larrue 2011, Kress and Horvitz 2005) or in secondary rain forests (Bito 2007). *Spathodea campanulata* has been highlighted by the Invasive Species Specialist Group as among ‘100 of the World’s Worst Invasive Alien Species’ (ISSG 2004).

Most invasive plants affect secondary forests, particularly in environments already highly disturbed by humans (Martin et al. 2008), but some invasive plants are able to grow in later-successional forests that have experienced little or no recent disturbance (Martin et al.

2004, Meyer and Florence 1996, Rejmánek 1996). These shade-tolerant plants, many of which are trees, pose a serious threat to the persistence of native forests (Martin et al. 2008, 2004, Meyer and Florence 1996). Therefore, it is especially important to identify potentially shade-tolerant plant invaders so that they can be targeted as priorities for prevention or control.

*Spathodea campanulata* is often described as a shade-intolerant invader (Francis and Lowe 2000, Martin et al. 2008, Thompson et al. 2007) but there is some controversy in the literature. Lambrada and DiazMedina (2009) report that the wind-dispersed seeds of *S. campanulata* are able to breach the 'barrier effect' of large trees present in edges of the forest, and these authors observed *S. campanulata* seedlings in native forests in Cuba, including primary forests. Other authors have suggested that *S. campanulata* seedlings are shade-tolerant and able to thrive without disturbance in rain forests (Anderson et al. 1992, Smith 1985, Staples and Cowie 2001). Little quantitative information is available on shade tolerance of *S. campanulata* seedlings, although such information is important for understanding invasion patterns and potential. Francis (1990) reported that *S. campanulata* seedlings grew well in ~50% shade, developing true leaves within 2 months. Labrada and DiazMedina (2009) indicated that the shade or semi shade of coffee plantations is the most favourable light environment for *S. campanulata* seed germination in Cuba and noted that higher seed germination occurs in semi-shade (~50% shade) than in full sunlight, but no attempt was made to assess growth at lower light levels. In this study, we examined field distribution patterns and photosynthetic and growth capacities of *S. campanulata* seedlings on Oahu and Hawaii (Hawaiian Islands) in order to characterize and quantify the light environments under which *S. campanulata* seedlings are currently establishing and capable of growing.

## Materials and Methods

**Field study sites**

The volcanic islands of Oahu and Hawaii (Hawaiian Islands) are found in the Pacific Ocean between 18°54′41″-21°42′34″ N, and 154°48′29″-158°16′46″ W. The island of Oahu ranges from sea level to 1,220 m asl with a land surface of 1,545.3 $km^2$; the island of Hawaii occupies an area of 10,432 $km^2$ with a highest summit at 4,205 m asl (State of Hawaii Data Book 2004). Both islands have a leeward dry side and a windward wetter side exposed to the dominant north-eastern trade winds. The mean annual rainfall in the surveyed area of Oahu ranges from 2,001 to 2,750 mm, and from 3,551 to 4,400 mm for the Hawaii site (Giambelluca et al. 2011).

The most important invasion of *S. campanulata* is observed between sea level and 226 m asl on the windward coast of Oahu and up to 312 m asl in Hawaii, in the “moderately dry-moist seasonal zone” and “lowlands rainforest zone” (Mueller-Dombois 2002). Study sites were located on the windward side, at the foot of the Ko’olau mountains (island of Oahu) and on the gentle downslope of Mauna Kea (island of Hawaii) in the lowland rainforest zone (Fig.1). In these wet forests, some native species remain (e.g., *Psychotria mariniana* (Rubiaceae), *Freycinetia arborea* (Pandanaceae), *Metrosideros polymorpha* (Myrtaceae), and *Syzygium sandwicensis* (Myrtaceae)), but the forests are now dominated by *S. campanulata* and other introduced trees species, e.g., *Cecropia peltata* (Urticaceae), *Aleurites moluccana* (Euphobiaceae), *Cinnamomum burmannii* (Lauraceae), *Falcataria moluccana* (Fabaceae), *Psidium cattleianum* (Myrtaceae), and *Schefflera actinophylla* (Araliaceae).

<Figure 1. near here>

**Study species**

*Spathodea campanulata* is a large evergreen tree, 20-25 m in height (Keay 1957, Neal 1948, Smith 1985) but sometimes reaching more than 30 m (Unwin 1920), with a dense irregular crown and a trunk diameter of 0.5-1.75 m (Holdridge 1942, Little and Skolmen 1989). This species grows rapidly (Francis 1990, Pacific Islands Ecosystems at Risk 2011; around 2 m per year in young stands (S. Larrue, personal observation)) and produces numerous red-orange flowers pollinated by bats and birds in its native range (Keay 1957). The species requires cross-pollination (Bittencourt et al. 2003); the fruit is a brown pod containing about 500 wind-dispersed seeds (Fosberg et al. 1993, Little and Skolmen 1989). Mature individuals of *S. campanulata* produce many pods, with 125,000 (Holdridge 1942) to 290,000 (Francis and Rodríguez 1993) seeds $kg^{-1}$ of pods. The species is mainly propagated by seeds, which can travel long distances (Francis 1990, Little and Skolmen 1989, Staples et al. 2000).

The native geographic area of *S. campanulata* extends from the west coast of Africa to central Africa between 12°N and 12°S (Irvine 1961). The tropical climate of the native range of African tulip tree is warm and wet, with a monthly mean temperature of 27°C to 30°C and abundant rainfall (Francis 1990). *Spathodea campanulata* has a broad ecological range (Florence 1997, Francis 1990) and therefore has been successfully grown throughout the tropics (Bärtels 1993, Francis 1990). It can survive in areas with a dry season of 1-3 mo; successful reproduction is reported at a minimum of 1,300 mm of mean annual precipitation. Substrate can be basic or acid soils, from clayey soil to loamy sands, with poor to excessive soil drainage (Francis 1990). The species is frost sensitive (Eliovson 1969) and apparently needs nearly full sunlight for reproduction (Little and Skolmen 1989).

In *c*. 1915, *S. campanulata* was introduced as an ornamental tree on Oahu (Staples and Herbst 2005). It is currently naturalized in lowland coastal plains on the windward side of the islands of Kauai, Oahu, Molokai, Maui and Hawaii (Wagner et al. 1999). In the Hawaiian Islands, *S. campanulata* ranges from sea level up to 1,000 m asl (Smith 1985). It is also found from sea level to 1,200 m asl in Puerto Rico (Francis 1990) and up to 1,430 m asl in the main island of

Tahiti (Society Islands, French Polynesia) (Meyer, pers. comm.). In Hawaii, Smith (1985) reported major infestations in almost every rainforest in East Maui and along the valley of northern and eastern slopes of Kauai and Oahu. Loope et al. wrote (1992, p. 567): “It [*S. campanulata*] should be monitored and opportunistically controlled in conjunction with systematic control of strawberry guava and other rainforest weeds.”

### Plot-based seedling counts and photosynthetically active radiation

Field studies were conducted from January-February, 2012. In forests with canopy dominated by *S. campanulata*, three 150 $m^2$ field plots were delineated. In the plots, we counted (1) the number of seedlings (< 30 cm height) positioned in 1-$m^2$ quadrats (n = 150 per plot), and (2) recorded the photosynthetically active radiation (PAR) in each 1 $m^2$ quadrat (systematic random sample). The PAR was recorded with a 0.3-m line sensor (Fieldscout PARmeter, Spectrum Technologies) at the centre of every 1 $m^2$ quadrat at 40 cm above the ground (± 10 cm). The PAR measurements in the three plots were made between 12h00 and 13h00 (i.e. near solar noon) during cloudless days. PAR was also measured in full sunlight at around 12h30 (± 3.5 µmol photons $m^{-2} \cdot s^{-1}$).

### Interpolation of PAR

In order to map the light environment and estimate the mean light environment in the three plots between 12h00 and 13h00, field light readings were entered into a Geographic Information System (see Figure 2; Geographic Information System Mapinfo Professional v.10, Interpolation Method). We then superimposed positions of the *S. campanulata* seedlings onto these plot maps and extracted the projected mid-day PAR value for each seedling.

<Figure 2. near here>

### Photosynthetically active radiation recorded along the line transect

In order to quantify seedling establishment across a wider range of light environments (including mid-day full sun), *S. campanulata* seedlings were surveyed along an abandoned section of roadside (1,590 m of length, Old Auloa Road, Oahu; both ends of road transect: 21°22'17.96" N-157°47'05.34" W, and 21°22'22.65"N-157°47'29.55"W). We recorded the PAR (between 12h00 and 13h00) above each *S. campanulata* seedling (< 30 cm height) encountered between 0 and 2 m from the roadside and compared the distribution of light readings at the seedlings to the distribution of available light environments along the roadside (random points ~ 30 cm above the ground).

### Correlation between spatial pattern of seedlings and PAR values

In order to test any correlation between photosynthetically active radiation and the spatial pattern and abundance of *S. campanulata* seedlings, we conducted the following analysis: We compared the distribution of PAR readings among the three plots and along the line transect to the distribution PAR readings at *S. campanulata* seedlings using a Kolmogorov-Smirnov test (XLStat® software, version 2007.6). We then tested whether some light environments are more frequently colonized by seedlings than expected. We compared these results to the photosynthetic responses of *S. campanulata* seedlings in controlled light environments.

### Photosynthetic and growth responses of seedlings

Ten seedlings were excavated from shaded or partially shaded environments located near the beginning of the survey transect. Seedlings were transported to the laboratory for photosynthetic measurements after allowing 2-5 days for recovery from any potential shock of transplantation. A chlorophyll fluorometer (PAM 2500, Heinz Walz GmbH) was used to measure the minimum saturating light level ($E_k$) for ten seedlings. Additionally, photosynthetic measurements were made between 10h00 and 14h00 with a photosynthesis meter (CI 340, CID Bio-Science, Inc.) and light response curves were used to estimate the light compensation point (minimum light required for plant maintenance). In order to confirm results from lab-transported field seedlings, additional light response curves were recorded directly in the field for seven seedlings found growing naturally in shaded environments.

To measure seedling growth rates in response to shade, lab-germinated seeds were transplanted into 16 cm conetainers containing a 3:1 mixture of Premier Promix Bx Mycorrhizae (Premier Tech Horticulture) and small black cinders (< 2.5 cm, Niu) with fertilizer (Osmocote 14-14-14 NPK, 0.055 g). Seedlings were placed on an outdoor bench in sun (n = 5, mean daily PAR 1300 μmol photons $m^{-2} \cdot s^{-1}$, range 143 to 2156) or shade (n=6, mean daily PAR 138 μmol photons $m^{-2} \cdot s^{-1}$, range 6 to 276) and grown under well-watered conditions until reaching the four-leaf stage (28-78 days, mean 56 days), at which time seedlings were harvested to determine relative growth rates, based on total dry mass.

## Results

### Plot characteristics and seedling abundance

All three plots were dominated by mature *S. campanulata* with flowers and pods, although a few other introduced woody species were also recorded (Table 1). A total of 97 *S. campanulata* seedlings were found. Seedlings height ranged from 3 to 18 cm with a mean height of 10 cm. Among plots, *S. campanulata* seedling density ranged from 0.04 to 0.54-m² (Table 1). The local-scale light environment within the three plots, as characterized by mid-day PAR measurements, ranged from 1% full sunlight (observed in all three plots) to 58.7% full sunlight (plot 3). Among the three surveyed plots, the median light environment ranged from 1% to 4.1% full sunlight (Table 1).

<Table 1. near here>

**Spatial pattern of seedlings and distribution of PAR values in the plots**

The overall distribution of seedlings among light environments differed significantly from the distribution of available light environments in the plots (Kolmogorov-Smirnov test, maximum distance = 0.541, $P < 0.001$). This difference in distributions was examined more closely by grouping PAR values into categories and plotting expected frequency of seedling occurrence (frequency of light environments in the plots) versus actual frequency of seedling occurrence among light environments in the plots (Figure 3). Within the lowest light ranges (< 20 µmol photons $m^{-2}\cdot s^{-1}$), seedlings are under-represented, whereas they are well represented or over-represented at the midday ranges of 51-200 µmol photons $m^{-2}\cdot s^{-1}$ (Figure 3) suggesting that this latter range may be a preferred light environment.

**Seedlings and distribution of PAR values along the line transect**

Along the line transect, 255 *S. campanulata* seedlings were recorded, ranging from 4 to 27 cm in height with a mean height of 12.5 cm. The midday PAR values above seedlings ranged from 0.4% to 100% full sunlight (1895 µmol photons $m^{-2}\cdot s^{-1}$), and the median PAR was 193 µmol photons $m^{-2}\cdot s^{-1}$. The midday light environments along the line transect estimated by 102 random points, ranged from 10 to 1319 µmol photons $m^{-2}\cdot s^{-1}$.

Along the line transect, the highest *S. campanulata* seedling densities occurred within the ranges of 50-150 µmol photons $m^{-2}\cdot s^{-1}$midday PAR (Figure 4). The PAR readings from random points along the transect demonstrate the seedling dis-proportionately occupy low light environments (Figure 4). Among the observed 255 seedlings on the transect, only three seedlings were found in full sunlight (between 1888 and 1895 PAR).

<Fig. 3 near here>

<Fig. 4 near here>

**Photosynthetic and growth rate measurements**

Field-collected seedlings averaged 7.6 cm tall (range = 3-14.5 cm) with an average of 5.7 leaves (range = 4-8). Overall, net photosynthetic rates of the seedlings were relatively low, with a maximum of around 3 µmol $CO_2$ $m^{-2} \cdot s^{-1}$ (Figure 5). Nevertheless, seedlings consistently had positive photosynthetic rates down to 50 µmol photons $m^{-2} \cdot s^{-1}$. The estimated compensation point was 10 µmol photons $m^{-2} \cdot s^{-1}$ (x-intercept of Figure 5). The results of photosynthetic measurements on naturally established field seedlings growing in shade were similar: the estimated compensation point was around 10 µmol photons $m^{-2} \cdot s^{-1}$, the net photosynthetic rates of the seedlings were around 2.5 µmol CO2 $m^{-2} \cdot s^{-1}$ (Figure 6).

Minimum saturating light ($E_k$) determined from chlorophyll fluorescence averaged 260 µmol photons $m^{-2} \cdot s^{-1}$ (range = 178-375 µmol photons $m^{-2} \cdot s^{-1}$) and this corresponds closely with the minimum saturating light as seen from lab-transported seedlings (180-400 µmol photons $m^{-2} \cdot s^{-1}$, Figure 5) and field-measured seedlings (~150 µmol photons $m^{-2} \cdot s^{-1}$, Figure 6). Average relative growth rate of sun-grown seedlings was not statistically greater than that of shade-grown (~10% full sun) seedlings (Figure 7).

<Fig. 5 near here>

<Fig. 6 near here>

## Discussion

Our results show that seedlings in the field were tolerant of mid-day PAR levels of < 50 µmol photons $m^{-2} \cdot s^{-1}$ (Figures 2-3), but the most frequent environment for *S. campanulata* seedlings was between 50 and 200 µmol photons $m^{-2} \cdot s^{-1}$ (Figure 3 and 4). These results show that seedlings commonly colonize light environments between 2.5-10% of full sun in the field. Shade environments have been defined as 4%-10% of full sun (Denslow et al. 1990, Kitajima

1994, Baruch et al. 2000 Schumacher et al. 2008). Therefore, we classify many of these *S. campanulata* seedlings as growing in shaded environments. Nevertheless, it must be acknowledged that mid-day point measurements of PAR provide only a rough snapshot of the daily light environment in the understorey. Seedlings may experience extreme fluctuation in light conditions from long periods of low light alternating with brief, unpredictable periods of high light during sunflecks (see e.g., Canham et al. 1990, Chazdon 1988, Leakey et al. 2005, Pearcy et al. 1994, Rijkers et al. 2000). Consequently, our mid-day PAR measurements may underestimate light availability to some *S. campanulata* seedlings during other parts of the day, while for other seedlings, our mid-day PAR estimates may represent maximum PAR availability, with lower PAR available in other parts of the day. Because of the inability of mid-day PAR measurements to capture potential variability in PAR throughout the day, it is important to also compare seedling photosynthetic responses to varying light availability. Shade-grown seedlings had net carbon gains from photosynthesis at very low light levels (50-100 μmol photons $m^{-2}{\cdot}s^{-1}$ PAR), and of particular interest was the fact that these shade-grown seedlings had low light saturation levels (Figures 4 and 5), suggesting that they would not benefit much from brief exposure to bright sunflecks.

Many tree species with little to no shade tolerance are known to support a "seedling bank" in a shaded understory, but these seedlings do not survive for long (Kobe et al. 1995). Based on our measurements of net productivity ($CO_2$ fixation) even at very low light levels, we expect long-term *S. campanulata* survival and slow growth under shaded forest conditions. In fact, in a separate field experiment, among freshly germinating seeds, seedling survival after one year under < 25% canopy openness averaged 38% (J. Bufford, unpublished data), which is high considering the many possible sources of early seedling mortality in the field. Furthermore, our observations in and around the field plots revealed evidence that a few saplings (< 5 m) were able to emerge from the understory shrub layer in shaded environments (Table 1), though these represent only a small proportion of the potential establishment indicated by much higher seedling abundance (Table 1; see Plot 3). Our findings lead us to classify *S. campanulata* seedlings as shade-tolerant.

Considering that saturating photosynthesis in the *S. campanulata* seedlings occurred at around 260 µmol photons $m^{-2} \cdot s^{-1}$, it is remarkable that a few seedlings were also found in completely open conditions on the line transect (Fig. 4). However, these full sun conditions likely existed only for a short time around mid-day, as tall vegetation surrounding these seedlings would have shaded them before and after mid-day. There is an overall inverse correlation between the number of seedlings and mid-day PAR values along the line transect (Spearman's, $r_s$= -0.356, p <0.0001) implying that full sun is a non-preferred environment. Lambrada and DiazMedina (2009) reported that the greatest abundance of young *S. campanulata* was recorded in areas of abandoned coffee plantations, which indicates that the shade or semi-shade conditions of these plantations is a suitable habitat for *S. campanulata* growth. Overall, these results suggest that a minimum level of shade is beneficial for *S. campanulata* germination and early seedling growth, although it seems likely that larger plants can take advantage of higher light conditions. For example, in a separate field experiment, one plant in a sunny environment was observed to flower within one year after germination, while no *S. campanulata* seedlings in the shade reached maturity within a year (J. Bufford, unpublished data).

We have assumed that light environment is an important factor in early recruitment of *S. campanulata* seedlings, but other causal factors such as disease or seed dispersal patterns might be correlated with light environments and might therefore contribute to observed patterns of *S. campanulata* recruitment and invasion. Low soil water availability may also contribute to the low number of *S. campanulata* seedlings in high light environments.

However, potted seedlings grown in full sunlight and watered regularly took as long or longer to develop (compared to shaded plants) (Figure 7), and these sun-grown seedlings generally had smaller, discolored leaves, with lower chlorophyll content (J. Bufford, unpublished data). It seems likely that temperature stress and/or reduced humidity become an important limitation under higher PAR conditions. We observed no signs of seedling predation at our field sites, while herviory at other field sites on Oahu averaged < 10% of leaf area (J. Bufford, personal observations).

Given that our plots were dominated by adult *Spathodea*, observed *S. campanulata* seedling densities might be considered rather low, ranging from 0.04 to 0.54 seedlings $m^{-2}$ (Table 1). In plots 1 and 2, light availability was very low (1 to 1.4% of full sun respectively; see Table 1) and the ground was nearly bare, with no seedlings other than *S. campanulata*. These plots show the limited recruitment of *S. campanulata* (i.e., seed germination and established seedlings) in such extremely shaded environments. In contrast, in plot 3, the mean mid-day light environment was 4.1% of full sun (Table 1) and the ground was covered by herbaceous plants 0.4 to 0.6 m in height. In this plot, the 'low density' of *S. campanulata* seedlings may be explained by high competition for space at ground level.

This research demonstrated the frequent occurrence and persistence of *S. campanulata* seedlings in shaded environments in Hawaii. Both photosynthetic rates and growth rates indicate that *S. campanulata* seedlings can maintain growth at low light levels (1-5% of full sun). Light availabilities at the forest floor of lowland mesic forest in Hawaii were previously measured in the range of 1.5-3.8% of full sun (Pearcy 1983), implying vulnerability to invasion, but light availability in the understory of different tropical rainforests can vary significantly (Brenes-Arguedas et al. 2011, Chazdon and Fetcher 1984, Condit et al. 2000, Torquebiau 1988, Wright and Schaik 1994) and may be as low as 0.48% in some regions of the world (e.g., Chazdon and Fetcher 1984). Nevertheless, the demonstrated ability of *S. campanulata* seedlings to maintain net carbon assimilation rates under very low light, together with the plant's strong capacity for dispersal by wind, should be considered in managing *S. campanulata* and assessing its risk of invading forests across the tropics.

**Acknowledgements**

We are grateful to the "Maison des Sciences de l'Homme" (MSH Clermond-Ferrand, France) and the "Secrétariat Permanent pour le Pacifique, section Fonds Pacifique" (Paris, France) for their substantial financial support for this research. We also thank two reviewers for their comments. JLB was supported by a graduate research fellowship from the National Science Foundation (Arlington, Virginia, USA).

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# FIGURES AND CAPTIONS

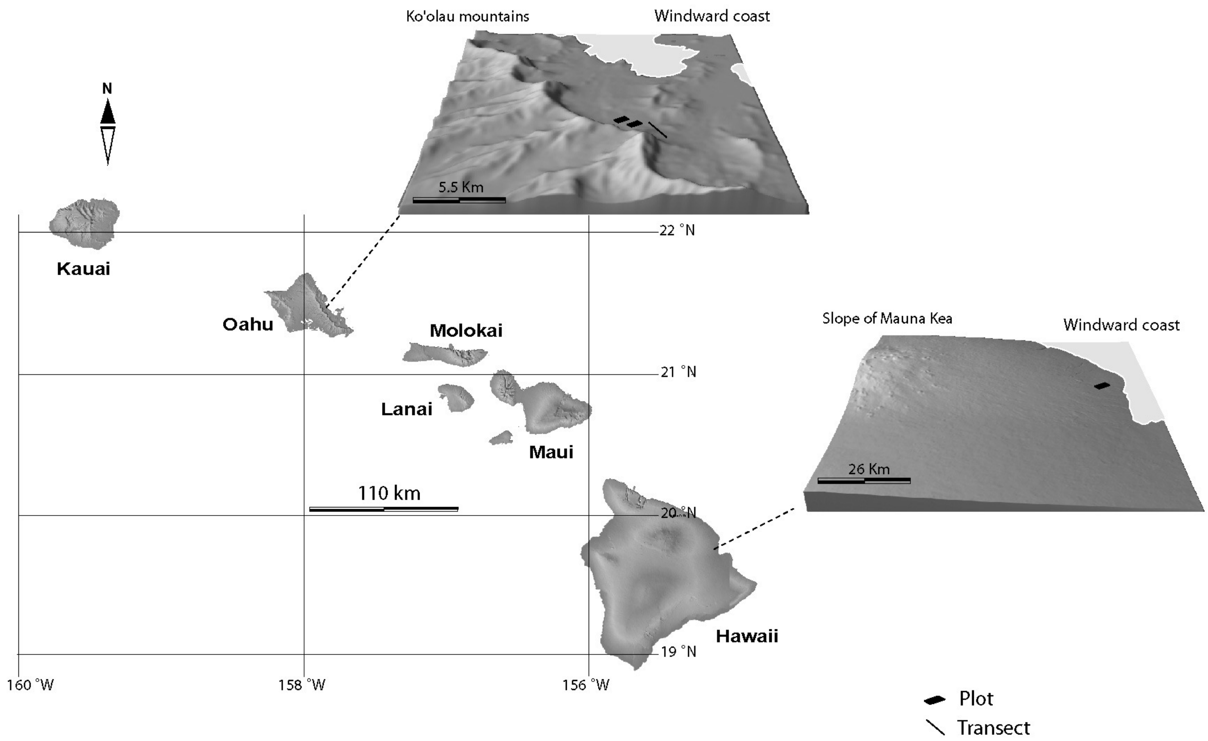


Figure 1. Location of study sites on the islands of Oahu and Hawaii (Hawaiian Islands).

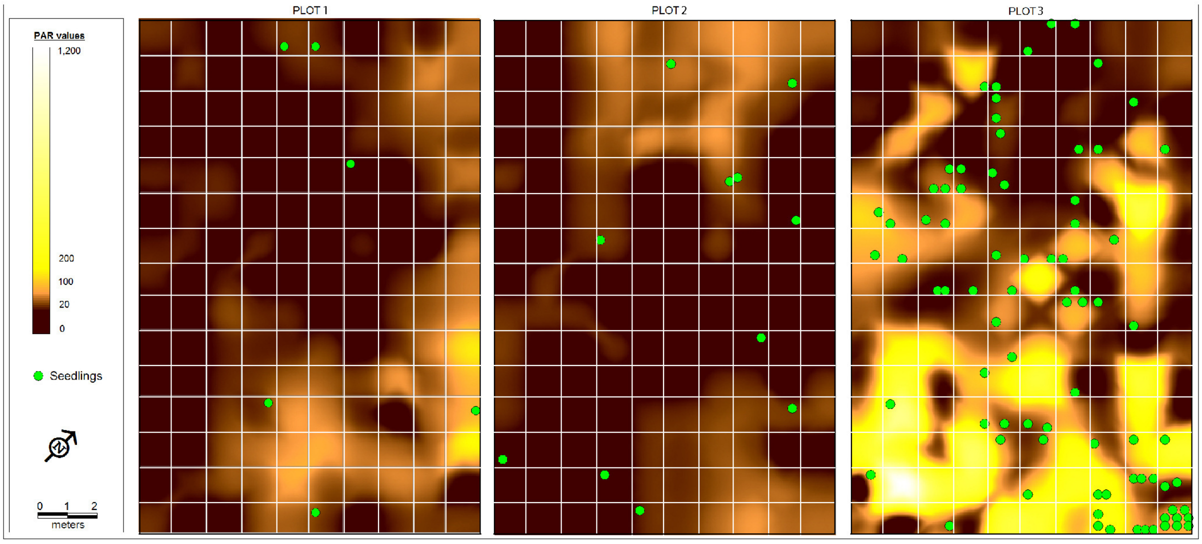


Figure 2. Spatial pattern of seedlings (mean height 10 cm) and photosynthetically active radiation (PAR) in closed forests (plots 1 and 2) and tree grove (plot 3) near solar noon as estimated by interpolation (GIS Mapinfo Professional v.10).

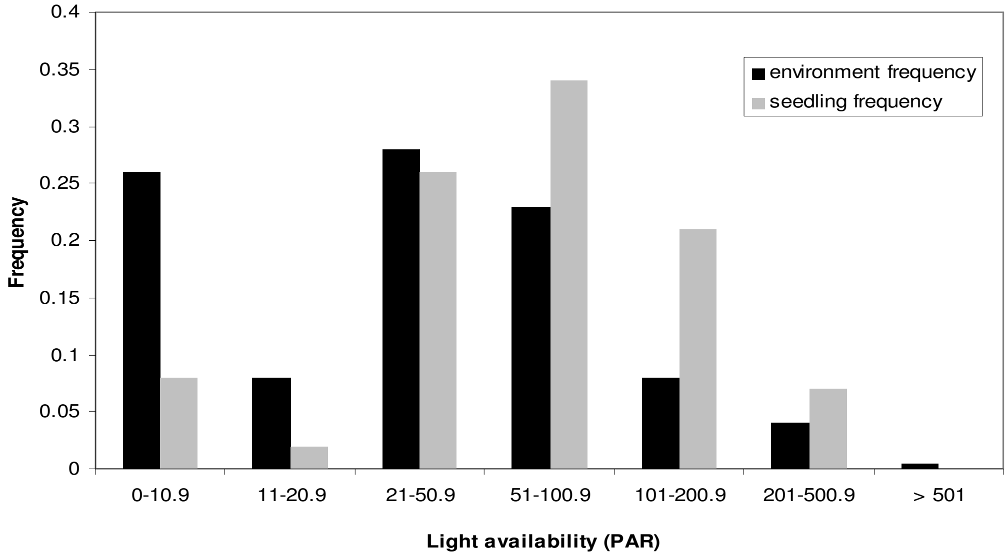


Figure 3. Distribution of light environments in the plots as compared to distribution of *Spathodea campanulata* seedlings (mean height 10 cm) among those light environments (n = 97 seedlings).

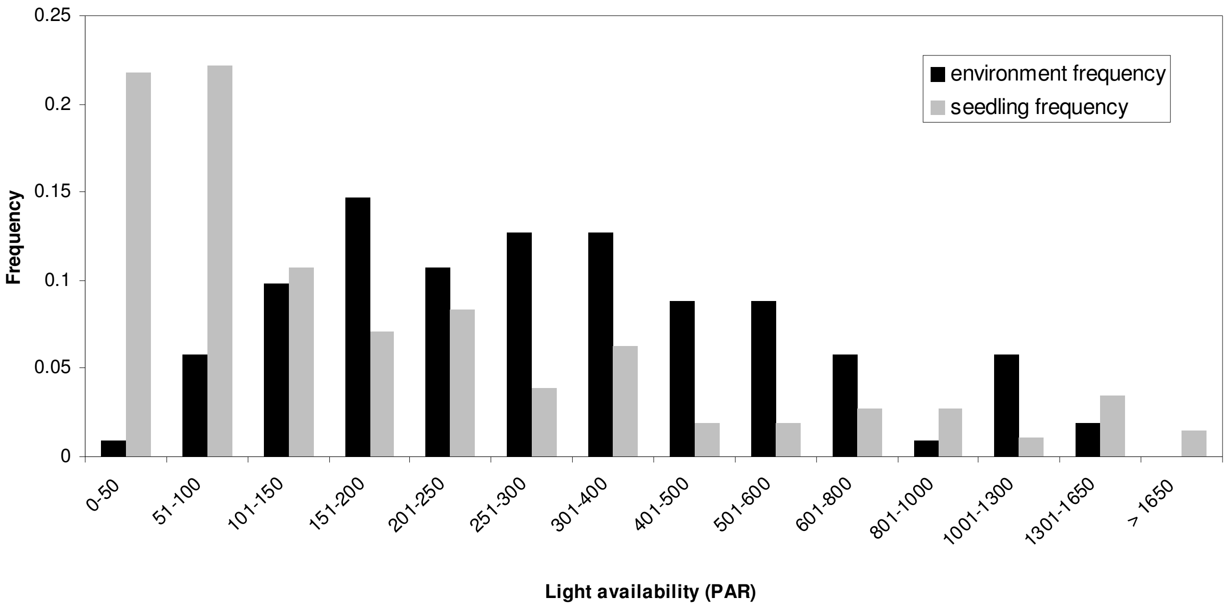


Figure 4. Distribution of light environments (random points) along a 1.5-km line transect as compared to distribution of *Spathodea campanulata* seedling (mean height 12.5 cm) frequency (n = 255 seedlings).

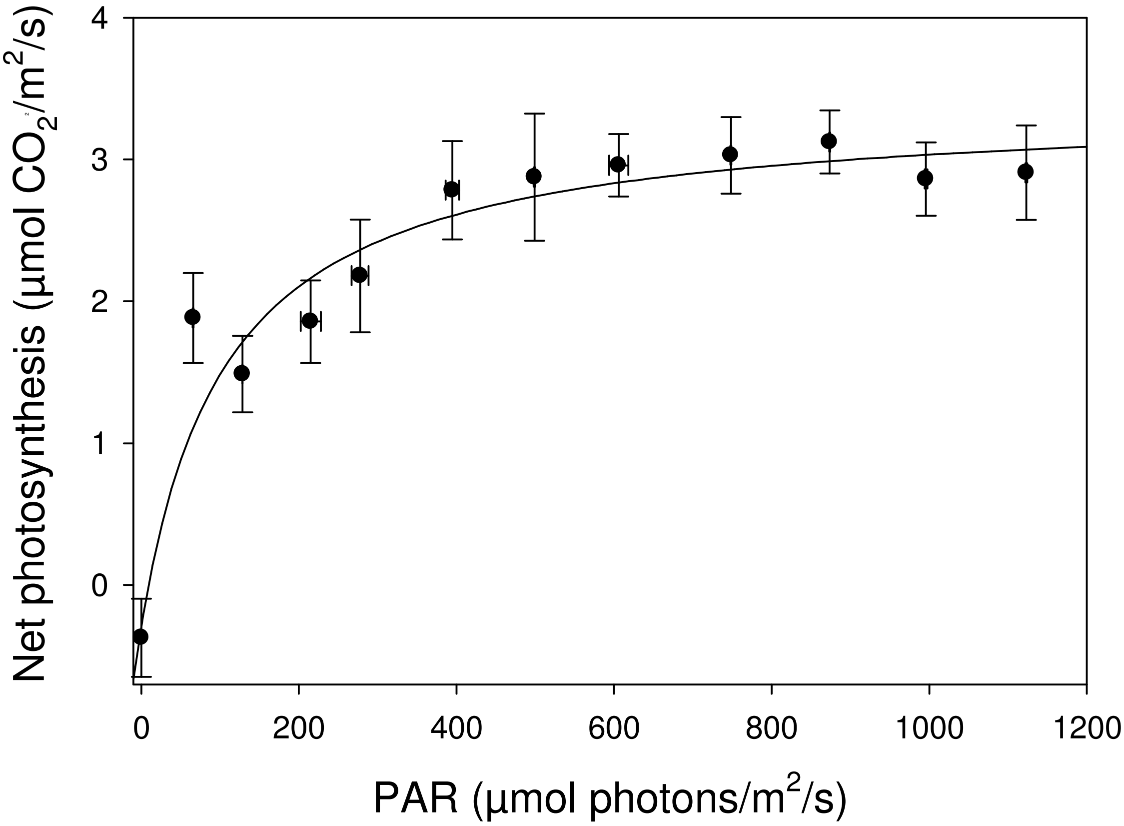


Figure 5. Light response curve for *Spathodea campanulata* seedlings (mean height 7.5 cm). Error bars indicate ± 1 SE (n = 10 seedlings).

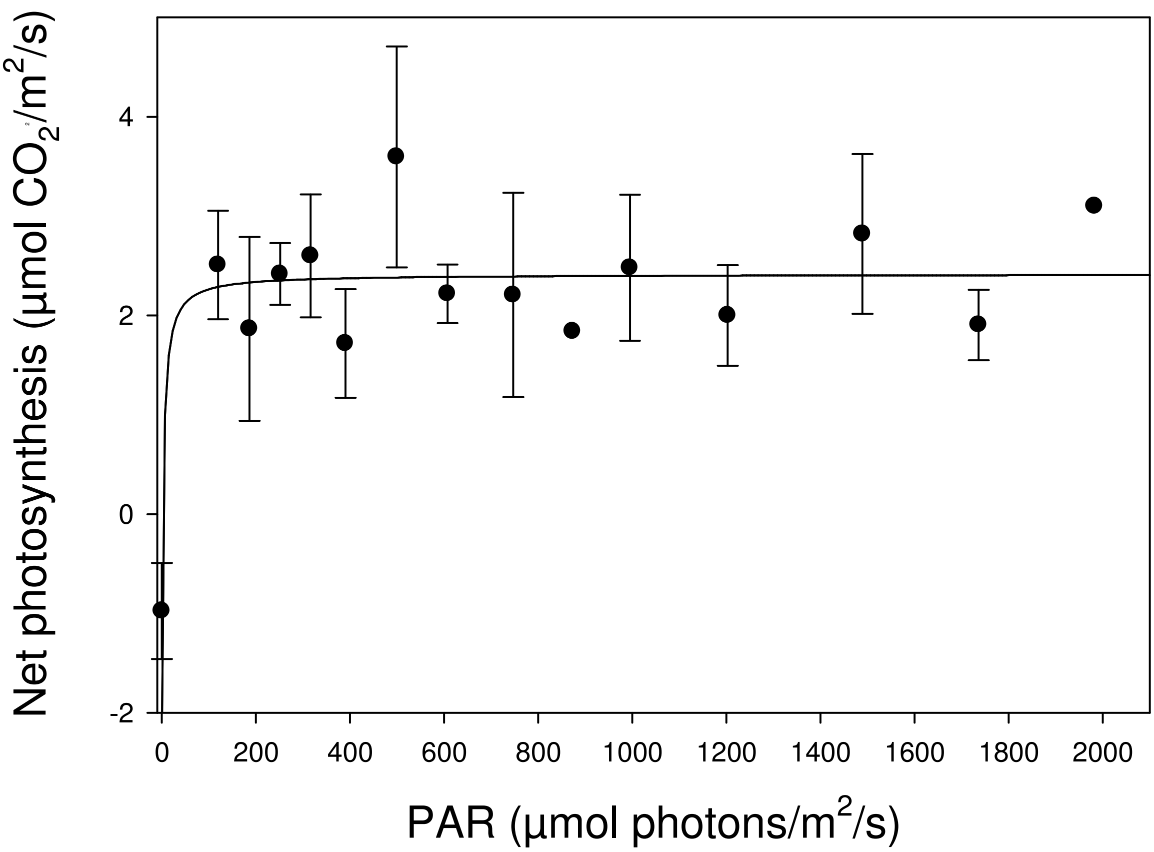


Figure 6. Light response curve for *Spathodea campanulata* seedlings (n = 7 seedlings; mean height 11 cm) naturally established in shade (mid-day PAR ranging from 1-150 µmol photons $m^{-2} \cdot s^{-1}$).

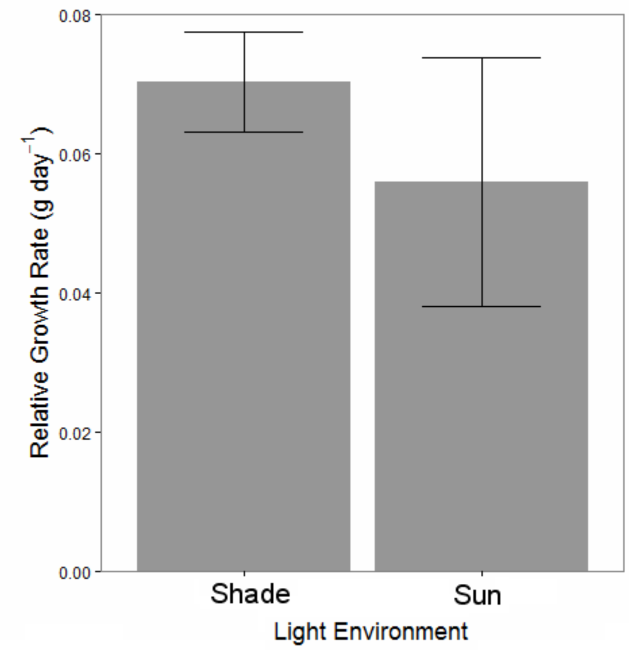


Figure 7. Average relative growth rate from seed to seedling with four true leaves in shaded (10% light) and full light environments. Seedlings were grown in containers with ample water. There was no statistical difference in growth rates between environments. Error bars indicate SE.

TABLE

**Table 1**. Characteristics of the plots (150 m²) with GPS coordinates, elevation, dominant trees, number and density of seedlings, and light environment.

| Plots | **1. Closed forest (Plot 1)** | **2. Closed forest (Plot 2)** | **3. Trees grove (Plot 3)** |
|---|---|---|---|
| Central Elevation | 126 m | 123 m | 117 m |
| Central GPS point | 21°22.22'05"N / 157°47'30.40"W | 21°22.22'30"N / 157°47'29.75"W | 19°52'0.576"N / 155°06'41.95"W |
| **Dominant trees (> 15 m)** | | | |
| *Spathodea campanulata* (Bignoniaceae) | 14 | 18 | 7 |
| *Leucaena leucocephala* (Mimosaceae) | | | 2 |
| **Trees species under canopy (1-5 m)** | | | |
| *S. campanulata* | 3 | 3 | 4 |
| *Hibiscus tiliaceus* (Malvaceae) | 1 | | |
| *Syzygium cumini* (Myrtaceae) | 1 | 1 | |
| *Persea americana* (Lauraceae) | 2 | 1 | |
| *Cinnamomum burmannii* (Lauraceae) | 1 | 1 | |
| *Psidium guajava* (Myrtaceae) | | | 1 |
| **Light environment in the plots** | | | |
| *Perception of visual light environment* | ***Deep shade*** | ***Deep shade*** | ***Shade*** |
| Range of PAR (µmol photons/m2/s) | 0 - 77.9 | 0 - 139.6 | 0 - 1,107 |
| Median PAR (PAR full sun: 1,884 ± 3.5 (100%)) | 19.4 (1%) | 27.3 (1.4%) | 77.3 (4.1%) |
| **Seedlings in the plots** | | | |
| Total of *S. campanulata* seedlings (mean height 10 cm) | **6** | **11** | **80** |
| Density (Seedlings/m²) | 0.04 | 0.07 | 0.54 |
| Range of PAR (µmol photons/m2/s) | 11.7 - 109 | 1 - 61.1 | 1.4 - 412.8 |
| Median PAR of the seedlings | 45.9 | 37.2 | 76.5 |